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STUDIES ON THE CUTANEOUS INNERVATION  
OF LIZARDS<sup>1</sup>

By

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INTRODUCTION

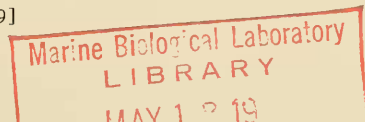
Since the appearance of Boeke's summary article (1934) on the comparative anatomy of the sense organs and Jaburek's (1926) classical contribution on the nerve endings in the reptilian epidermis, there have been but few—and these inconclusive—articles on the subject of the innervation of reptilian skin. The task of interpreting and describing the innervation of the reptilian skin has been greatly facilitated by the recent excellent studies on the structure of reptilian skin by Maderson (1965a).

For the past decade in our laboratory we have investigated and reported upon the innervation of the skin, deep connective tissues, bones, and the heart of man and a variety of mammals (Miller and Kasahara, 1964, 1963; Miller *et al.*, 1960; Ralston *et al.*, 1960; Miller and Kasahara, 1959a, 1959b; Miller *et al.*, 1958). This experience in the techniques of staining nerve endings and in the interpretation of neurohistological structure has been of great benefit in the study of reptilian skin innervation.

MATERIALS AND METHODS

General skin structure was studied by fixing pieces of skin from freshly sacrificed animals in 10 percent neutral formalin or Bouin's solution. After paraffin embedding and sectioning, the tissues were stained using a variety of procedures (hematoxylin and eosin, iron hematoxylin aniline blue, and van Gieson's being the usual stains used to study the epidermal and dermal elements).

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Nerve fibers and endings were demonstrated in some cases by staining formalin-fixed skin according to Bodian's Protargol Method. Silver staining of nerve fibers is particularly useful to demonstrate the relationship of nerve fibers and endings to other cellular elements. In the great majority of cases, nerve fibers and endings were demonstrated by methylene blue staining. In our experience we achieved better results with simple methylene blue immersion rather than with intracardiac perfusion. Fairly large ( $2 \times 2$  cm.) segments of skin from which most of the underlying muscle and subcutaneous tissue had been carefully removed were immersed in 0.01 percent methylene blue in physiological saline solution for 20 to 30 minutes. To prevent the skin piece from curling, it was often stretched and pinned on a small cork strip, and the cork and the skin both immersed in the methylene blue solution. After immersion, the skin strips were exposed to the air for 3 to 5 minutes and then placed in chilled ( $40^{\circ}$  F.) 8 percent ammonium molybdate overnight. The next day, the skin pieces were washed in six changes of iced tap water over a period of 60 minutes, rapidly dehydrated in ethyl alcohol, cleared in xylene, and then placed, stored, and studied in benzyl benzoate.

Skin from the following species was studied:

Iguanidae

*Anolis carolinensis*

*Sator grandaevus*

*Sceloporus occidentalis*

Agamidae

*Agama agilis*

*Calotes versicolor*

Anguidae

*Gerrhonotus multicarinatus*

Varanidae

*Varanus bengalensis*

*Varanus griseus*

Gekkonidae

*Gecko gecko*

*Hemidactylus species*

*Phelsuma madagascariensis*

*Teratoscincus scincus*

Scincidae

*Liolopisma laterale*

Xantusiidae

*Xantusia vigilis*

OBSERVATIONS

To understand best the cutaneous innervation of lizards, or for that matter,

the skin of any vertebrate, one must establish a point of reference. As is the case for many other anatomical systems, the innervation of the skin of man and mammals has been much more studied and is better understood than it is in that of any other vertebrate group.

Figures 1 and 2 present in diagrammatic fashion the essential features of the innervation of human skin. In figure 1 the pattern of innervation of glabrous or nonhairy skin is presented. Here, one sees that a basic triad of nerve endings are related in a specific way to the epidermal and dermal elements. From small myelinated nerve fibers there are simple tapering unbranched or few branched terminals—these are the so-called free-fiber nerve endings. In man and mammals these terminals extend between the lower epidermal cellular layers and usually terminate in the stratum granulosum. These type nerve endings are also abundant in the dermal connective tissue. From medium-sized myelinated nerve fibers, endings with enlarged or expanded tips end in close apposition to a specialized undersurface of the lowermost layer of cells of the stratum germinativum (the combination of an expanded-tip nerve ending in association with a specialized epithelial cell constitutes the so-called Merkel's disc). In the glabrous skin of man, groups of expanded-tip endings are usually associated with the basal epidermal cells in the sweat gland ridge areas. In the dermis of the glabrous skin, as well as in many connective tissue areas of the mammalian organism, groups of expanded-tip type endings form a category of what one may term complex unencapsulated endings. In the human glabrous dermis, the Ruffini ending is a typical representative of this type of ending. Complex unencapsulated endings in the connective tissues of fasciae, aponeuroses, tendons, joint capsules, and periosteum make up the so-called "stretch receptors."

Encapsulated endings derived from medium-sized myelinated nerve fibers occur in the dermal papillae (Meissner's corpuscles), just under the epidermis (Krause end bulbs), or in the deeper dermis (Vater-Pacinian corpuscles).

In the hair-covered skin of man and mammals (fig. 2) one finds the same triad of nerve endings that occurs in the naked skin, but in the hairy skin the endings are related differently to the skin and hair elements. Free-fiber terminals extend and end between the lower epidermal cell layers, terminate in the dermal connective tissue, and are found in the connective tissue sheath of the hair follicle. Expanded tip or complex unencapsulated nerve endings are associated only with the cells of the outer root sheath of the hair follicle, and never with the epidermis proper. As a rule, neither complex unencapsulated nor encapsulated nerve endings are found in the hairy skin. The skin of the human breast is an exception to this rule, however (Miller and Kasahara, 1959).

Observations on the skin of mammals other than man reveals that the innervation of the hair-covered skin is very similar to that of man. In specialized areas, such as in snouts and footpads, there are certain variations in the nature of the innervation. A good example is the abundance of expanded-tip type end-

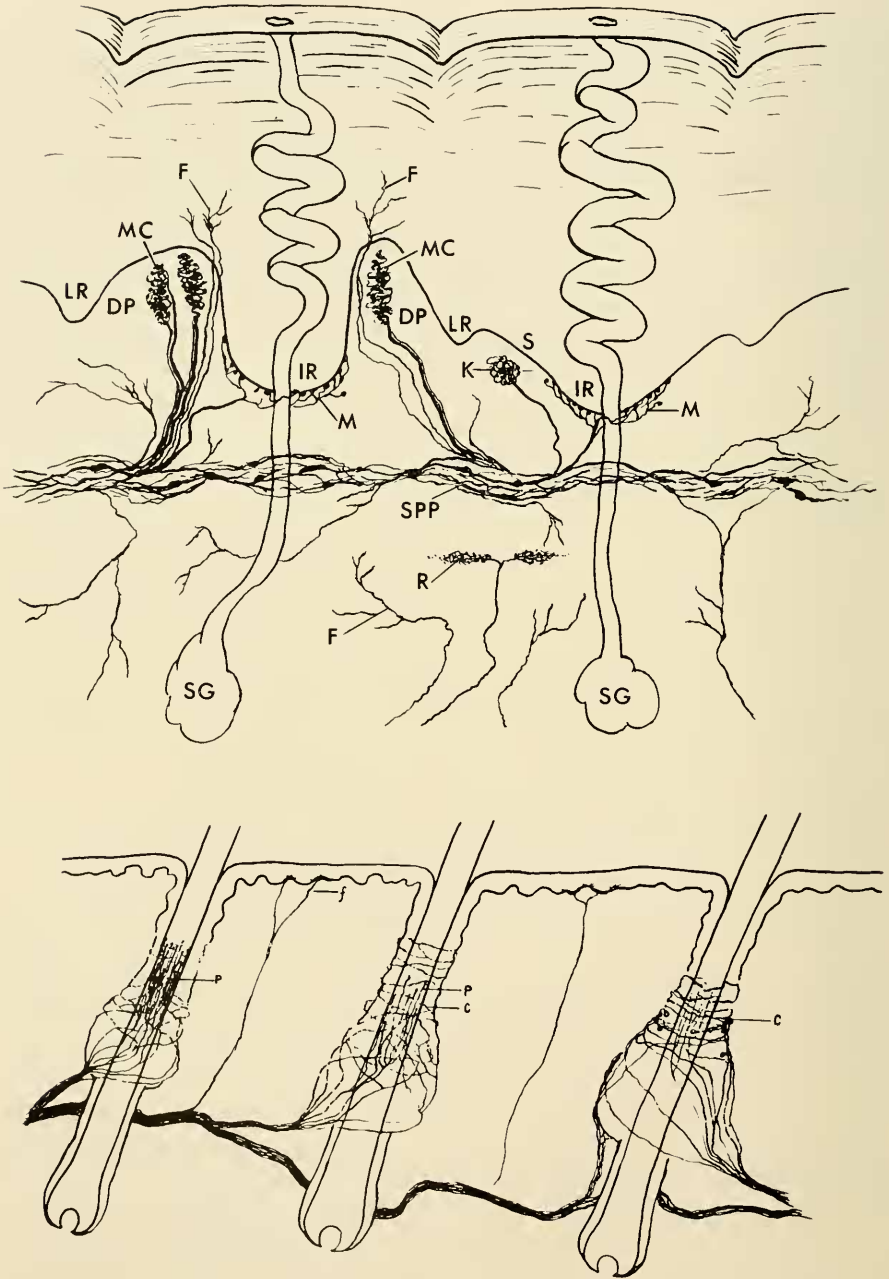


FIGURE 1. A diagrammatic vertical section of the epidermis and underlying dermis and the associated nerve endings in the human fingertip. Two papillary ridges are shown. Two sweat glands (SG) are shown in the dermis. Their ducts proceed toward the skin surface

ings that are associated with the epithelial cells of snout tissue, or with the "Eimer's" organ of the mole's nose.

The cutaneum of lizards is different from that of mammals in that there are no hairs (properly speaking) and the lizard scale is a modified type of glabrous skin. The essential skin elements are an underlying dermis of variable thickness overlaid by a basically three-layered epidermis. Depending on the physiological state of the skin, the epidermis may be composed of but three layers, or, just before sloughing, the epidermal elements may be duplicated (Maderson, 1965b). The epidermis consists of a basal layer of living cells, few or several cell layers thick, a loose or alpha keratin layer in the middle, and on the surface, a more dense beta keratin layer.

Just as in any vertebrate animal, the nerve fibers that supply the cutaneum form a plexus in the deeper portion of the cutis. The road map-like pattern of the cutaneous nerve plexus is demonstrated in figure 4.

The same basic triad of nerve endings that are found in the skin of man and mammals are found in the skin of lizards. The exact form, disposition, and pattern of arrangement of the nerve endings are somewhat different, however (compare figs. 1, 2, and 3).

Small tapered nonexpanded free-fiber nerve endings that are so common in

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and enter the base of the intermediate epidermal ridge (IR). The coiled sweat-gland duct progresses upward through the epidermal strata and opens in the central portion of the papillary ridge. The epidermis extends most deeply into the dermis in the region of the intermediate ridge (IR). At the lateral edge of the papillary ridge is another epidermal ridge projecting into the dermis, the limiting (LR) or anchoring ridge. The upward dermal projections between the intermediate and lateral ridges form the dermal papillae (DP). A dermal papilla is seen on each side of intermediate ridge of left papillary ridge. Dividing the papillary dermis transversely are septa (S) connecting the intermediate and limiting ridges. Partitions may further subdivide the papillae.

Ruffini endings (R) are found in the dermis. Free nerve endings (f) are encountered in the dermis, the dermal papillae, and the epidermis. Krause end bulbs (K) are usually located just under the epidermis. Meissner's corpuscles (C) occur in the dermal papillae. Merkel's discs (M) are closely associated with the lowermost layer of cells of the epidermis in the region of the intermediate ridge (IR) and the septa (S). SPP is the subpapillary plexus.

This figure is adapted from figure 1 in Miller *et al.*, 1960, and reproduced with permission of the authors and Pergamon Press.

FIGURE 2. A diagrammatic vertical section of the hairy skin of the human extremities showing the relation of the nerve endings to the epidermis and hair follicles. Free nerve endings (f) are seen terminating in the shallow dermal papillae or between the epidermal cells. The hair follicle is innervated by both the freely terminating tips of the branches of the circular (C) fibers and the expanded tips of the palisade (P) fibers. The hair follicle on the right shows some expanded tips associated with the circular fibers, an uncommon occurrence.

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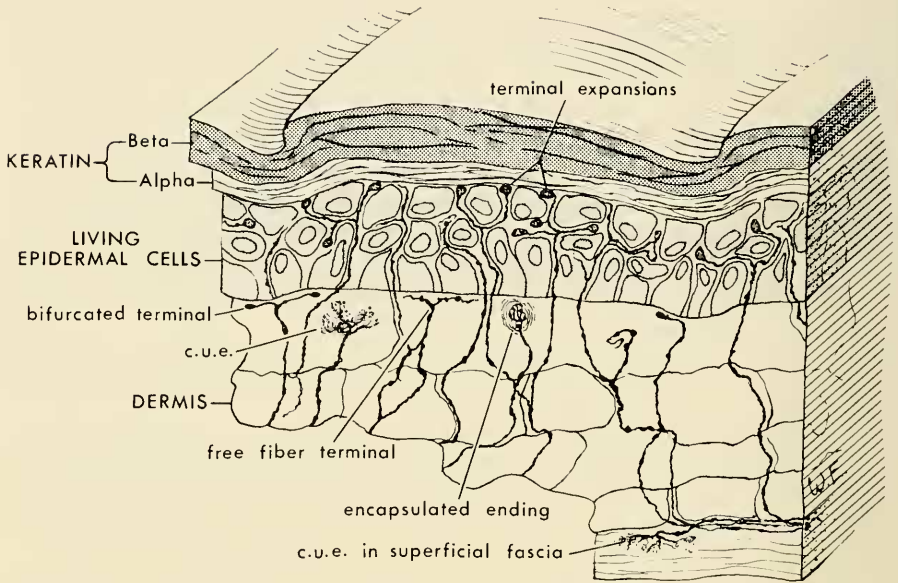


FIGURE 3. A diagrammatic vertical section of the epidermis and underlying dermis in a lizard. This is a composite representation and while all the following types of nerve endings might be found in one area, specific types of endings are usually more abundant in some parts of the body than in other areas.

Extending into and ending between the living epidermal cell layers are expanded-tip nerve endings (terminal expansions). These terminal intraepidermal expansions are relatively large and are abundant in all reptilian epidermis. In the dermis are free-fiber terminals; these are the endings of small- to medium-sized myelinated nerves that end as simple tapered nonexpanded tips, and occasionally may extend into the lower epidermal cell layer.

In the upper portion of the dermis directly below the hinge region (area between two scales) is a nerve ending labeled (bifurcated terminal). In the hinge area to the right is a simple terminal (unlabeled). These nerve endings may be small encapsulated nerve endings (see text).

The structures labeled (C. U. E.) are complex unencapsulated nerve endings and are found in the dermis and deeper body connective tissues.

An encapsulated nerve ending is labeled in the upper dermis. Such nerve endings are usually found only in the dermal tissue of the head area.

the epidermis of man and mammals occur frequently in the dermis of lizards (figs. 12 and 13), but only infrequently extend into the epidermis. As occurs in man and mammals, however, small free-fiber endings are abundant in all the deeper connective tissues of both somatic and visceral structures.

It might be interjected at this point that we have never observed sensory endings of amyelinated fibers in the cutaneum of either reptiles or mammals, but have found such terminals in the deeper connective tissues of both these animal groups.

The most abundantly occurring type of nerve ending in the skin of lizards is one derived from small- to medium-sized myelinated nerve fibers which originate in the subcutaneous plexus and then project into the epidermis (figs. 5-8). The terminals of these nerve fibers may be one or several quite large expanded tips that are most frequently located between the epidermal cells of the uppermost layers of the living cell layer of the epidermis. Many fibers, however, form expansions along the course of the nerve fiber so that some terminal expansions do occur in the lower layers of the epidermis.

In our opinion, the terminal expansions bear no special relationship to the epidermal cells, and are, therefore, unlike the Merkel's discs of mammalian skin where the epithelial cells are modified at the point where they contact an expanded nerve terminal. Jaburek (1926), in his classical article on the nerve endings in reptilian skin, expounds at great length on the intracellular location of the expanded-tip endings. While it did not appear to us that either the nerve fibers or the nerve terminals were intracellularly located, Munger (1965) has shown recently in ultrastructural studies of the Merkel's discs in the opossum snout that intraepidermal nerve fibers may be enclosed by epidermal cell processes in much the same way as amyelinated neurones are ensheathed by Schwann cells.

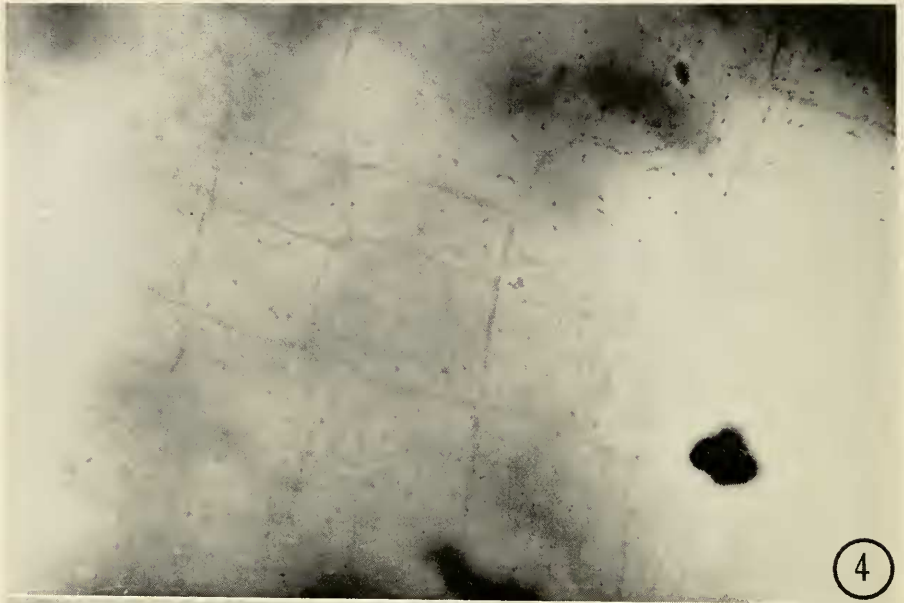
The exact relationships of the intraepithelial nerve fibers and endings and the epidermal cells in reptiles will not be determined until ultrastructural investigations are undertaken.

In the absence of experimental evidence, it is not possible to say whether the intraepidermal expanded-tip nerve endings of lizards (and other reptiles as well, Jaburek, 1926) are functionally homologous to the tapered-tip free-fiber endings of the mammalian epidermis, or, are rather more related to the Merkel's discs which are associated with the underside of the human epidermis, or the epidermal cell layers of mammalian snout tissue. The possible functional capacities of these fibers are discussed below.

For the time being we shall refer to the intraepithelial nerve endings of reptiles as expanded-tip terminals and not assume any structural or functional correlation with mammalian type nerve endings.

The intraepithelial expanded-tip endings seem to be more abundant in the scales of the head and shoulders, but are found over the entire body. It is interesting that the specialized "sensory spots" of the varanid lizards are well endowed with expanded-tip terminals (fig. 7). More concerning these specialized areas will be described below.

We have observed a peculiar type of nerve ending that seems to be most common in the dermis of the hinge region (the area between any two scales). This ending is a simple or bifurcated structure and is derived from a medium-sized myelinated fiber (fig. 14). This ending sometimes appears to have a halo about it as though it were an encapsulated ending. Thus, it may be closely





analogous to the Meissner's corpuscle or Krause end bulb of the mammalian dermis.

Complex unencapsulated endings are found in the dermis, subcutaneous tissue, fascial sheets, and perimysium of lizards (figs. 15-17). These endings, both structurally and in their location, are almost identical to those found in man and mammals (see Ralston *et al.*, 1960), and are shown in the turtle, *Trionix sinensis*, by Hin-Ching and Maneely, 1962.

Encapsulated nerve endings remarkably similar to those found in mammalian tissues are present in the deep dermal tissues in the region of the eyelids, ventral lips, and snout of lizards (figs. 18-20). Other than in these areas, encapsulated nerve endings have not been found in the cutaneum of lizards. They are probably widely distributed throughout the deeper connective tissues of the lizard body as they are in mammals, but we have not investigated this point in lizards.

The glabrous skin of primates and certain other mammals have modifications in the form of dermal papillae. These are projections of dermal connective tissue (fig. 1) into bays or indentations of the epidermis which contain both vascular and neural elements. Most primate dermal papillae contain encapsulated nerve endings of the Meissner corpuscle type.

The skin of reptiles does not possess dermal papillae, but has specialized areas which, while not structurally homologous to the dermal papillae, are probably functionally similar.

Such specialized "tactile" or "sensory" spots have been described in a wide variety of reptiles (Maurer, 1895; Plate, 1924; Jaburek, 1926). In general, these areas consist of localized groups of epidermal cells that are much taller and better innervated than the surrounding unmodified epidermis, and the overlying keratinized skin layers are either thinner or thicker than in the unspecialized skin, or form "hair-like" projections.

From our experience we believe that the "sensory" structures vary mainly according to the modification of the keratinized cells that overlie the specialized underlying columnar epithelial cells. If the overlying keratinized layer is thin and a depressed area is formed, one might refer to this structure as a "sensory pore" (as found in *Sator* and *Xantusia*). If the overlying keratinized layer, particularly the beta keratin is thickened, a "sensory plaque" is formed (this

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FIGURE 4. *Phelsuma madagascariensis*. Methylene blue.  $\times 225$ . The deep dermal plexus of nerve fibers from which nerves are supplied to the dermis and epidermis.

FIGURE 5. *Varanus griseus*. Methylene blue.  $\times 450$ . Expanded-tip nerve endings in the upper portion of the living cell layer of the epidermis from a ventral body scale. Note that the nerve fibers may have expansions along their course, but that the largest expansions are usually terminal and the highest in location. Compare this frontal view with a longitudinal skin section in figure 6.

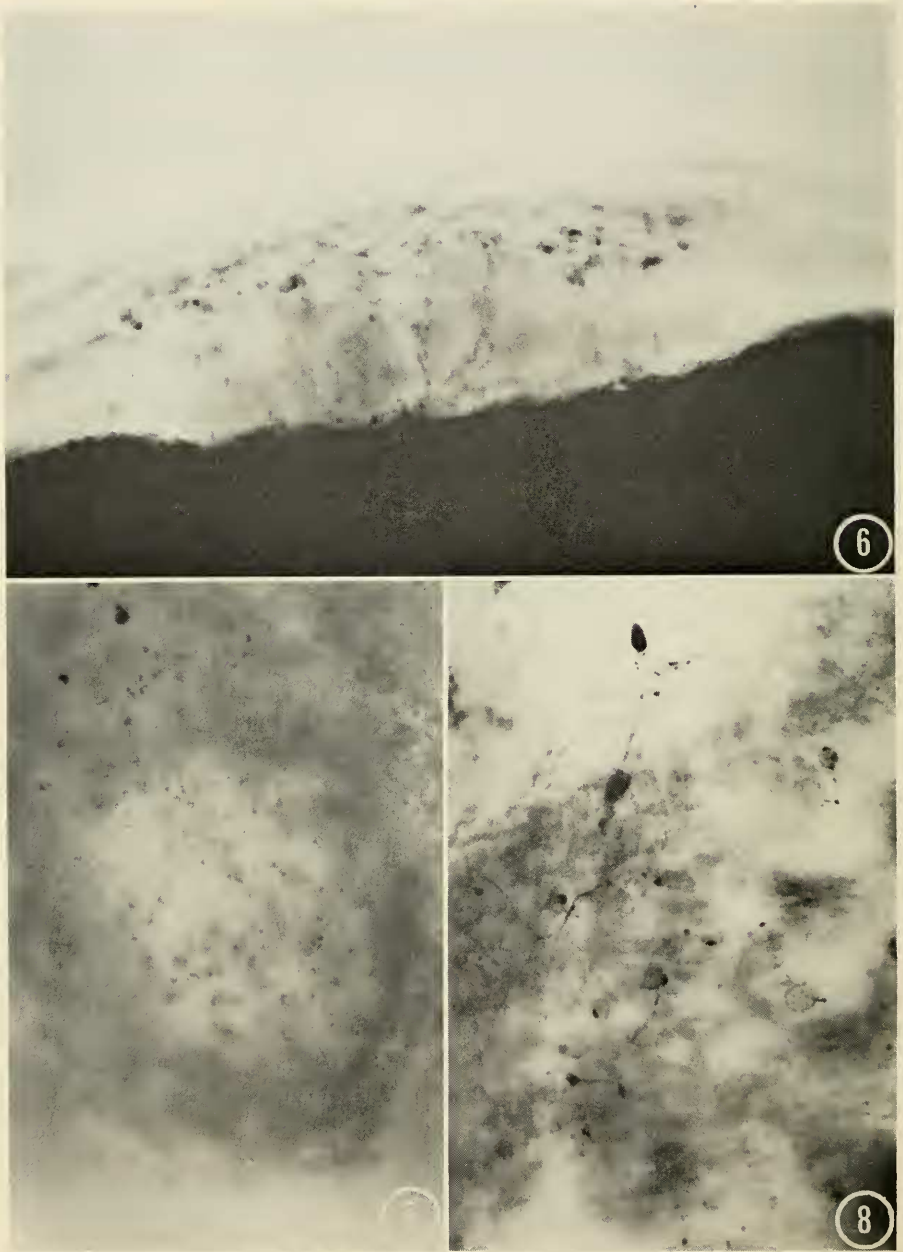


FIGURE 6. *Varanus griseus*. Methylene blue.  $\times 650$ . A longitudinal section through a specialized skin spot of a lip scale. The black area in the lower portion of the photograph is the dermis. Note the nerve fibers coursing upward through the living epidermal cell layers. Smaller expansions are observed in the course of the fibers as they extend upward.

structure is characteristically found in the scale of varanid lizards), or, if the keratinized epithelium forms a thin projecting bristle-like process, or processes, a "hair-like" organ is formed; the latter are characteristic of most agamids, some gekkonids, and a few iguanids. Further study of the detailed structure and the species distribution of specialized skin sensory areas is needed.

The "sensory plaques" of the varanid lizards are grossly visible lighter appearing circular areas. In the head region there may be one or several such areas within a single scale. In the lip scales there are three or more such specialized areas in each scale. However, on the body scales they appear singly and consistently at the caudal end of the scale. An ordinary histological section through such an area is seen in figures 9 and 10. One may observe that in the specialized area, the living epidermal cells are much taller than the ordinary epidermal cells. How else these epidermal cells may be modified is not demonstrable by light microscopy. These cells are very well innervated, and in essentially the same manner as are the nonspecialized epidermal cells (figs. 7 and 10). Perhaps the number of nerve fibers and endings is more abundant in these areas, but we have not made a quantitative study of this point.

Overlying the tall columnar cells of the varanid specialized area is a thin, loose, alpha keratin layer, and a thick, almost lenslike beta keratin layer. Because of the lenslike appearance of the beta keratin layer, one might postulate that this area might be sensitive to some type of radiant energy. On the other hand, this structure might serve no other function than that of a relatively sensitive tactile organ.

The "hair-like" organs of agamids, gekkonids, and iguanids are found usually near or on the scale edges and are characterized by a group of high cylindrical epidermal cells overlaid by a very specialized "hair-like" projection made up of the keratinized cell layers. In figure 11 the "hair" is seen to be separated from the underlying epithelial cells; this separation is artifactual due to the preparation of the sections, and actually, the keratinized "hair-like" process is firmly attached to the underlying columnar epidermal cells.

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The large expanded tips are seen near the top of the living cell layer, just beneath the alpha keratin layer. Compare with figure 5.

FIGURE 7. *Varanus griseus*. Methylene blue.  $\times 425$ . The circular area is a specialized skin "plaque" or spot characteristic of the varanid lizards. The overlying keratinized layers are more clear than in the surrounding unspecialized epidermis probably due to the more regular arrangement of the keratinized epithelial cells. The plane of focus is at the level of the uppermost living cell layer and here one sees numerous nerve fibers with their expanded-tip terminals ending between the tall columnar cells (compare with figures 9 and 10).

FIGURE 8. *Sator grandaevus*. Methylene blue.  $\times 525$ . The plane of focus is at the upper layer of living epidermal cells. Visible in the field are the expanded-tip endings of several fibers. With light microscopy we are unable to determine the exact nature of these nerve endings.

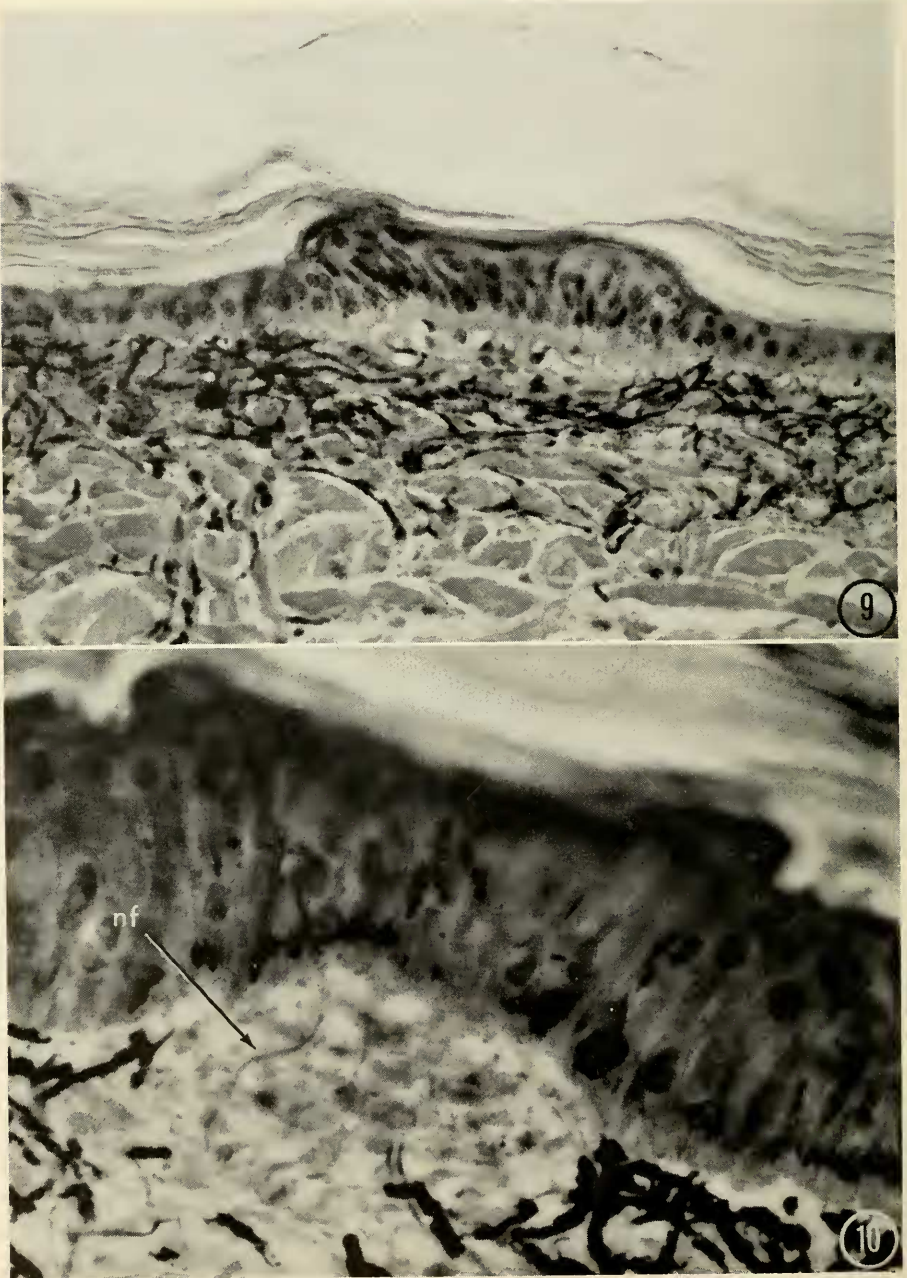


FIGURE 9. *Varanus bengalensis*. Van Gieson's stain.  $\times 425$ . Section through a specialized area of the skin near the pineal eye of a varanid lizard to show its structure. The living epidermal cell layer is clearly seen in the upper middle part of the photograph. Notice that

While expanded-tip nerve endings were observed to be abundant in the specialized living cell layer of the varanid sensory areas, we were not able to demonstrate such endings in the "hair-like" organs. Nerve fibers were seen supplying the base of the organ, but we did not see the terminals. However, we feel that the region of the epidermal cells of the "hair-like" organ is innervated in essentially the same way as any other specialized area.

#### DISCUSSION

The studies of Jaburek (1926) on the innervation of the skin of lizards, snakes, turtles, and the alligator, and those of Hulanicka (1913, 1914) on the skin of turtles and crocodiles are in essential agreement with our observations. In the skin of lizards, as well as in the skin of other reptiles, the most numerous nerve endings are the expanded-tip endings of small- to medium-sized myelinated fibers. These nerve terminals are found in the upper living cell layers of the epidermis over most of the reptilian body. In no other vertebrate order is there such an abundance nor so large expanded-tip type nerve endings found in the epidermis. This type of epidermal innervation is apparently unique to the reptiles.

Neither of the above workers (*op. cit.*) described nonexpanded tip (tapering terminals) endings in the reptilian epidermis, and we found them only infrequently. Thus, the common reptilian epidermal expanded-tip nerve ending is replaced in the mammalian epidermis, by a nonexpanded tip, or tapered-tip free-fiber ending. The comparative functional capacities of these types of nerve endings is discussed below.

Both Jaburek and Hulanicka (*op. cit.*) did describe Merkel-like tactile discs in the lower epidermal and upper dermal layers of turtles and snakes, but not in lizards. We also failed to find tactile discs in our lizard material.

As we found in the head region of lizards, Hulanicka (1913, 1914) also found encapsulated nerve endings in the head area of the crocodile and turtle.

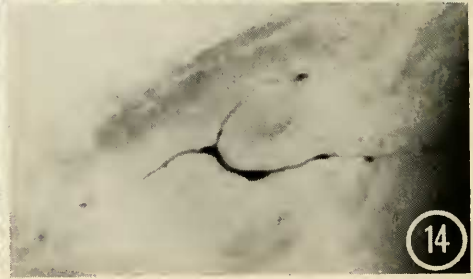
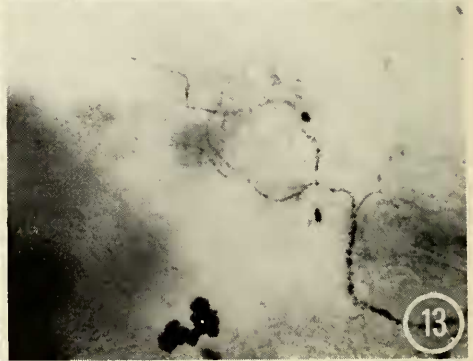
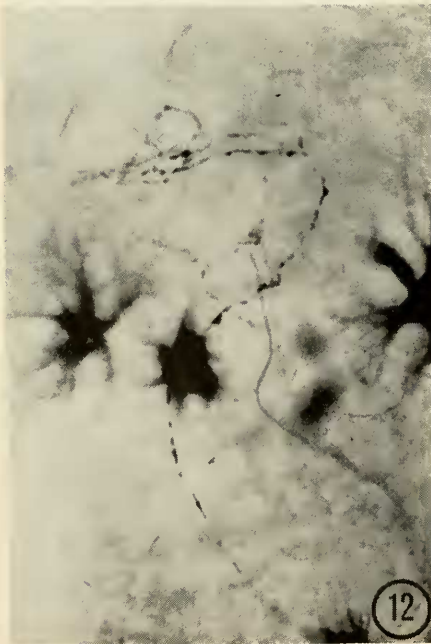
Jaburek (1926) and we both found that the specialized sensory skin organs of varanids are well innervated by expanded-tip nerve terminals. Jaburek also

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the cells of the specialized area in the upper center of the photo are much taller than the adjacent epithelial cells. Below the living epidermal cell layer is a relatively thick dermis with black-appearing processes of chromatophores in the upper dermis and heavy strands of collagen fibers coursing at right angles to one another making up the bulk of the dermis.

The middle, loose, or alpha keratin layer directly overlying the living cell epidermal cells is thinner over the specialized columnar cells, while the overlying beta keratin cell layers form a thicker, seemingly more regularly arranged "lenslike" area.

FIGURE 10. *Varanus bengalensis*. Bodian Protargol Silver.  $\times 950$ . A section through a specialized area of varanid skin showing silver-stained nerve fibers (nf) coursing upwards through the underlying dermis to supply the overlying specialized columnar sensory cells. Figure 7 shows the nerve terminals in such a specialized area.



shows that wherever such specialized areas are found in reptilian skin, the tall epidermal cells are abundantly innervated by expanded nerve terminals. While there is no experimental evidence to indicate what the possible function of the specialized areas in any reptile might be, the structure of these areas would suggest that they are most likely relatively sensitive tactile organs, functionally analogous to the mammalian dermal papillae with their contained Meissner's corpuscles. Further, the lenslike quality of the overlying beta keratin layer of the varanid organ has led us to speculate that these areas might also be sensitive to some type of radiant energy.

The general structure of the special "hair-like" organs of gekkonids, agamids, and some iguanids were much studied by Schmidt (1920), and more recently discussed by Elias and Bortner (1957). The innervation of the epithelial cells of the "hair-like" organs has not been well described, but we believe that they are innervated by the same type of expanded-tip terminals that one finds in the general living epithelial cells of reptiles.

For the moment we believe it most likely that when the "hair-like" projections are moved, a deformation of the underlying epidermal cells is produced, and the structure thus functions as a tactile organ.

While the specialized "hair-like" sense organs of certain lizards are made up of various epidermal components, just as is the true hair of mammals, we hesitate to homologize these structures. The lizard "hair-like" organs are similar in many ways to mammalian hairs, but they are found in species that are far removed from the ancestral mammal-like reptile. Because of the minor anatomical differences between these "hair-like" organs and mammalian hairs, we would rather consider them as closely analogous, and not homologous structures.

The argument in favor of the homologous nature of the "hair-like" organs of lizards and the mammalian hair is presented by Elias and Bortner (1957) and very completely discussed by Botezat (1914) and Maurer (1923).

Even in mammals we are not yet sure of the relationship between the types

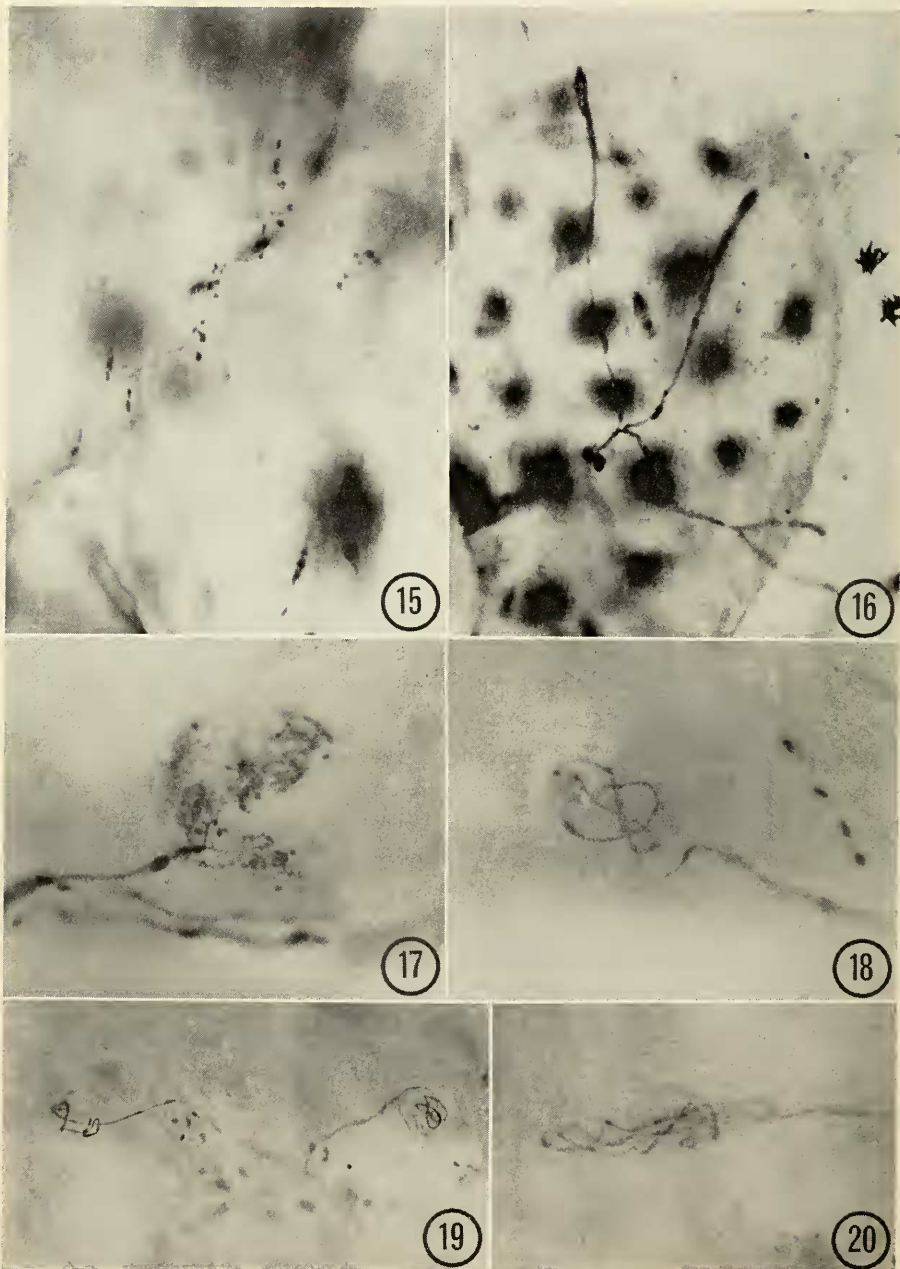
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FIGURE 11. *Calotes versicolor*. Bodian Protargol Silver.  $\times 300$ . A section through a lip scale to show the general structure of a "hair-like" organ. Note that the living epidermal cells in the "hair" region are tall columnar in shape. Formed from the overlying keratinized cell layers is a "hair-like" process. The space or separation between the keratinized layers and the living epithelial cells is artifactitious due to preparation of the section.

FIGURE 12. *Teratoscincus scincus*. Methylene blue.  $\times 400$ . A branched tapered-tip free-fiber terminal in the superficial dermis.

FIGURE 13. *Sator grandaevus*. Methylene blue.  $\times 250$ . Tapered-tip free-fiber nerve endings in the upper dermis. Sometimes these fibers may extend into the living epidermal cell layer.

FIGURE 14. *Xantusia vigilis*. Methylene blue.  $\times 650$ . A specialized nerve terminal in the upper dermis that may be an encapsulated type. Note the clear area or "halo" about the nerve tip. These endings are most frequently seen in the hinge region between two scales.





of nerve endings and their particular function. At the present time, the majority opinion (Rose and Mountcastle, 1959) holds that small myelinated or amyelinated free-fiber endings are related to pain phenomena, free-fiber endings of small myelinated fibers with thermal (heat and cold) perception, and tactile discs (Merkel's discs), complex unencapsulated endings, and encapsulated endings such as Meissner's corpuscles and Krause end bulbs with tactile sensibility, if peripheral in location, or with tissue position (proprioception) if more deeply located. Not only is there nerve ending specificity, but also the total pattern of innervation is important, and the central analysis of peripheral signals is as much dependent on receptors especially sensitive to different types of stimuli as it is to the spatial orientation of nerve endings.

While in man and mammals there are large numbers of small tapered-tip free endings located both in the epidermis and dermis, in reptiles we find but few such endings, and these are largely dermal in location. Physiological experiment indicates that such types of nerve endings are probably associated with pain and thermal sensibility in mammals. Since these types of endings are rarely observed in reptiles, one might conclude that these animals are relatively insensitive to pain, heat, or cold. Such an interpretation is probably unwarranted, and it would seem much more likely that the ubiquitous expanded-tip epidermal nerve endings of reptiles are capable of mediating several sensory modalities. This interpretation fits well with the observations of Weddell (1960) on corneal nerve endings and with those of Lele *et al.* (1958) on the innervation of the integument of the amphioxus. Until the somatic sensory capacities of reptiles are more thoroughly investigated, our understanding of the evolution of sensory mechanisms must necessarily remain speculative and incomplete.

We believe that the observation of greatest significance in this study of the innervation of the skin of lizards is that the same basic types of nerve endings are found in this order of reptiles that are found in the skin of man and other mammals. There are minor variations in the exact morphology of the types of specific nerve endings, and particularly, there is variation in the number and disposition of the nerve endings, but the same basic triad of small

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FIGURE 15. *Xantusia vigilis*. Methylene blue.  $\times 375$ . Complex unencapsulated endings in the connective tissue sheath or fascia overlying skeletal muscle fibers.

FIGURE 16. *Teratoscincus scincus*. Methylene blue.  $\times 200$ . Complex unencapsulated ending in deep dermal connective tissue of head region.

FIGURE 17. *Varanus griseus*. Methylene blue.  $\times 350$ . Complex unencapsulated ending in the deep dermal connective tissue of the ventral snout.

FIGURE 18. *Varanus griseus*. Methylene blue.  $\times 350$ . Encapsulated nerve ending in the dermal connective tissue of the ventral snout.

FIGURE 19. *Varanus griseus*. Methylene blue.  $\times 125$ . Encapsulated nerve ending in the connective tissue of the dermis of the eyelid.

FIGURE 20. *Varanus griseus*. Methylene blue.  $\times 175$ . Encapsulated nerve ending in the conjunctival connective tissue.

free-fiber, expanded-tip (complex unencapsulated), and encapsulated endings are found in both these groups of vertebrates.

Correlations between the different types of cutaneous nerve endings and their possible function is even more speculative in reptiles than it is in man and mammals. A great deal more structural, physiological, and psychological analysis is necessary before we may better correlate neural structure and function.

#### SUMMARY

The skin of lizards is innervated by the same basic types of nerve endings that are found in the skin of mammals. Tapered-tip or free-fiber terminals of small myelinated nerve fibers are common in the dermis and epidermis of mammals, but are infrequently observed in reptiles.

The most abundant nerve ending found in reptilian skin is derived from small- to medium-sized nerve fibers which extend into the living epidermal cell layer and terminate in the upper portion of the living cell layers in expanded-tip terminals. These terminals are apparently not associated with any epidermal cell modifications. Whether the intraepidermal terminals of reptiles are homologous to the intraepidermal tapered-tip endings of mammals is not known. While we did not observe any Merkel's disclike endings in lizard skin, these have been described by other workers in turtles and crocodiles. Complex unencapsulated nerve endings are present in the dermis as well as the deeper connective tissues. Encapsulated endings were observed in the dermis of the hinge region and the head.

Specialized "sensory" areas are common in a variety of lizards. In such areas, the living epidermal cells are taller than in the nonspecialized skin. These cells are well innervated by expanded-tip nerve terminals. The overlying keratinized layers in these specialized areas may be either thinner, or thicker, than in the unspecialized skin. In the varanid lizards the beta keratin layer is thick and the regularly arranged cells impart a "lenslike" quality to the structure.

"Hair-like" organs are found in most agamids, some gekkonids, and a few iguanid lizards. The living epidermal cells in these structures is high columnar and probably well innervated with expanded-tip terminals. The overlying keratinized epithelium forms a "hair-like" projection. The innervation of lizard skin is compared with that of mammalian skin and the possible functional capacities of the various nerve endings is discussed.

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